

Mesozoic echinoid diversity in Portugal: Investigating fossil record quality and environmental constraints on a regional scale



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ARTICLE INFO

Article history:

Received 21 October 2014

Received in revised form 4 February 2015

Accepted 11 February 2015

Available online 19 February 2015

Keywords:

Echinoid

Diversity

Sampling proxies

Fossil record

Portugal

ABSTRACT

Several analyses of diversity through geological time use global, synoptic databases, and this practice often makes it difficult to distinguish true signals in changing diversity from regional-scale sampling and/or geological artefacts. Here we investigate how echinoid diversity changed through the Mesozoic of the Lusitanian basin in Portugal based on a comprehensive, revised database, and seek to distinguish biological signal from geological or environmental constraints. The observed diversity pattern is far from having a defined trend, showing many fluctuations that appear to be linked with gaps in the geological record. This study revealed that, independently of the method used, whether correlation tests or model fitting, the diversity signal is not completely explained by the studied sampling proxies. Among the different proxies, marine facies variation in combination with outcrop area best explains the palaeodiversity curve.

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1. Introduction

A long-standing debate in current palaeobiological research concerns the significance of global diversity patterns retrieved from raw counts of fossils through time (e.g., Raup, 1972, 1976; Sepkoski et al., 1981; Smith, 2007a, 2007b; Benton et al., 2011; Hannisdal and Peters, 2011; McGowan and Smith, 2011; Benton et al., 2013; Brocklehurst and Fröbisch, 2014; Dunhill et al., 2014a, 2014b), and numerous quantitative studies of the quality of the fossil record have concluded that fossil diversity is biased by many factors.

Many studies have shown a strong correlation between global fossil diversity and numbers of fossil-bearing formations. This strong correlation has been interpreted in three distinct ways: (1) bias or 'megabias'; covariation between palaeodiversity and formation time series was formerly widely seen as key evidence for intrinsic deficiencies in the fossil and rock record (i.e., Peters and Foote, 2001, 2002; Wang and Dodson, 2006; Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011; Upchurch et al., 2011); (2) common cause; covariation between palaeodiversity and such geological signals as formation count or rock volume, could result from a single driver such as sea level change, prompting some

researchers to invoke a common cause model (Peters, 2005; Hannisdal and Peters, 2011); and (3) redundancy; palaeodiversity and fossil formation counts could be intimately linked because both metrics accumulate in tandem as a result of the ways in which palaeontologists assemble data through research time (Benton et al., 2011, 2013). In contrast to that strong relationship at global scale, studies performed at regional or local scale may find weak (Benton et al., 2004; Mander and Twitchett, 2008; Benton, 2012; Dunhill et al., 2012, 2013, 2014a, 2014b), or strong (Crampton et al., 2003; Smith and Benson, 2013) relationships between the two. If there truly are megabiases that can be measured by rock record proxies, then fine-scale investigation should reveal stronger correlations between alpha and beta diversity and the proxies than time series recorded at global scale, because statistical noise ought to be minimized, and thus evidence ought to emerge that one phenomenon drives the other.

Echinoderms, and especially echinoids, have a long collecting record and a wide geographical distribution. Their high-magnesium calcite endoskeletons, either articulated or disarticulated, can be found in different marine facies, and are widely represented in the fossil record. This might seem surprising because such mineralogy is unstable, but the recrystallization of high-magnesium to low-magnesium calcite during diagenesis does not result in loss or significant transformation of the ossicle structure. Echinoderms are characterized by their calcitic endoskeleton, which is relatively stable during diagenesis. The endoskeleton composition excludes the possibility of different preservation rates among different echinoderm groups. It is assumed that echinoid preservation

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potential is uniform, because the endoskeleton composition appears to be constant through time. This leads to good preservation of echinoids and easy collection from marine outcrops (Smith, 2007b).

Despite the high potential for preservation of echinoids, taphonomic bias, such as was noted by Smith (2007b), cannot be ruled out. After the death of an echinoderm, the soft tissues decompose in a few days. Without these tissues, the endoskeleton disaggregates and the ossicles are easily dissociated, which are often small and invisible to the naked eye. This might mean that species with larger macroscopic ossicles would be recognized in the field, while smaller ossicles would remain unnoticed.

Here, we choose to study a regionally restricted, but well sampled series of echinoid faunas from Portugal in order to control for certain biases. For example, Jackson and Johnson (2001) highlighted the geographical bias and the poor sampling of high-diversity, low-latitude marine faunas in global datasets. Further, the geological record of the Northern hemisphere is better studied than the Southern. Here, this geographical bias (Smith, 2007a) is avoided by focusing on one restricted area. Also, sampling efficiency issues (Smith, 2007a) are minimized in this study, because the database does not arise from compilation of the efforts of many investigators each, with different research strategies and collecting modes, but is based mostly on geological survey collections, which derive from comprehensive sampling by a limited number of collectors, trained to a particular search style, and covering the landscape equally and efficiently.

In the past, diversity analyses have been performed at different taxonomic levels (for example, species, Smith and Benson, 2013; genus, Dunhill et al., 2014a, 2014b; or family level, Jepson and Penney, 2007). The choice of which level to use seems arbitrary and greatly dependent on practical questions relating to the information that the authors could obtain. It is not axiomatic which level is most representative of the true diversity signal. Generally, the aim is to document an accurate species-level signal in order to understand macroevolution, so a family-level diversity plot would be regarded as likely to generalize the data too much to be useful. Palaeontologists have often preferred to compile their palaeodiversity data at generic, rather than species level, for two reasons (e.g., Foote and Sepkoski, 1999; Smith, 2007b; Mayhew et al., 2012; Smith et al., 2012; Dunhill et al., 2014a, 2014b): species-level compendia may show greater volatility, because new species are established more frequently than new genera; and species boundaries are often more debated than generic boundaries in the primary taxonomic literature.

Robeck et al. (2000) demonstrated that a finely subdivided taxonomic grouping provides a more precise sampled diversity analysis than coarser subdivisions. They concluded that the use of finer taxonomic divisions leads to a more precise measurement of the number of species recorded from the rock record than coarser divisions. The sampled diversity does not correspond to the real biological diversity, since it is not corrected for sampling problems.

The echinoid clade can be subdivided into two major subclades, the regulars and the irregulars. These two groups evolved at different times in the echinoid tree, with irregulars evolving from regular echinoids (Kroh and Smith, 2010). The evolution from one to the other allowed echinoids to occupy both soft sediment and higher energy habitats. In addition, the evolution and radiation from regulars to irregulars occurred during the time frame under study. Therefore, it is possible that the two groups have different diversity patterns in relation to environmental changes, making it worthwhile to investigate the diversity patterns of both.

Smith and Benson (2013) compared echinoid diversity in the Cretaceous of the U.K. against several rock and environmental proxies. They found a strong association between the palaeodiversity signal and a combination of outcrop area with marine facies. It would, therefore, be interesting to see whether their key conclusions are applicable to other regional studies of the same group, and the Portuguese echinoid record provides impetus for the present study.

The aim of this study is explore the nature of the Portuguese echinoid fossil record, by investigating the palaeodiversity signal and comparing it with the coeval, and already documented echinoderm record from the U.K. We will explore similarities and differences between the two records; similarities could represent true biological signals, or reflect the preservation conditions that influenced both areas. The marine Mesozoic succession in Portugal is ideal as the basis for a regional-scale case study on echinoderm fossil diversity because it has a well sampled Mesozoic fossil record, with more than 251 taxa represented around a thousand specimens in total, and it lies at the convergence of two oceanic realms (Tethys to the South and the North Atlantic to the West).

2. Materials and methods

2.1. Diversity curves

The diversity dataset comprises echinoid occurrences in the Portuguese fossil record from specimens in public collections. Prior to this analysis, all these occurrences were subjected to thorough alpha-taxonomic revision by B.C.P., based on examination of type specimens and original materials throughout, down to species level whenever possible (Appendix A). Because the dataset results from a taxonomic revision performed by a single person, and the revision has been done recently, this standardizes the species identification criteria and reduces the risk of taxonomic bias, as identified by Smith (2007a).

The analysed specimens comprise tests (complete and their fragments) and spine fragments (articulated and disarticulated). The vast majority of these specimens (around 95% of the observed fossils) are at the Museu Geológico (Lisbon, Portugal), comprising specimens from the Lusitanian and Algarve Basins. In addition, other Portuguese museums that have relevant Mesozoic echinoderm specimens, including the Museu Mineralógico e Geológico (Coimbra University, Portugal) and the Museu da Lourinhã (Lourinhã, Portugal) were also surveyed for specimens. The vast majority of the analysed taxa were collected during geological surveys of the Portuguese territory. This type of campaign should ensure equal sampling effort, through the different formations and localities, analogous to other such case studies based on geological survey collections and records from New Zealand (Crampton et al., 2003) and the United Kingdom (Dunhill et al., 2012, 2013, 2014a, 2014b). The argument is that geological survey palaeontologists collect every fossil they can find, even those of very poor quality, and will search every square kilometre of their mapping areas, thus ensuring a geographically evenly distributed sampling effort. In more usual situations, palaeontologists generally do not follow such a search model, but go straight to known, rich localities, and so over-collect where fossils are rich (the so-called “bonanza effect”; Raup, 1977), and under-collect where fossils have not yet been found. Similarly to this study, the diversity data used by Dunhill et al. (2012, 2013, 2014a, 2014b) were mainly based on information gathered by the British Geological Survey, with few additions from other sources. The correlation tests between diversity and sampling metrics in those studies could support either bonanza or bias effects, but information transfer statistical tests by Dunhill et al. (2014b, Fig. 4) indicate redundancy between the two metrics.

The specimens analysed in this work came from the Lusitanian (West of the Iberian Peninsula) and Algarve basins (Southwest of the Iberian Peninsula), corresponding to subsiding basins beside two passive continental margins (Fig. 1). The two basins are infilled with Mesozoic and Cenozoic sediments and their formation is linked with the opening of the Atlantic Ocean to the west, and the Tethys Ocean to the south. The Portuguese Mesozoic echinoid fauna comprises 251 species, after the mentioned taxonomic revision. This taxonomic revision resulted in the addition of 5 new taxa. From the 251 Portuguese taxa verified by the taxonomical revision, 197 species possessed tests and were found in the Lusitanian basin.

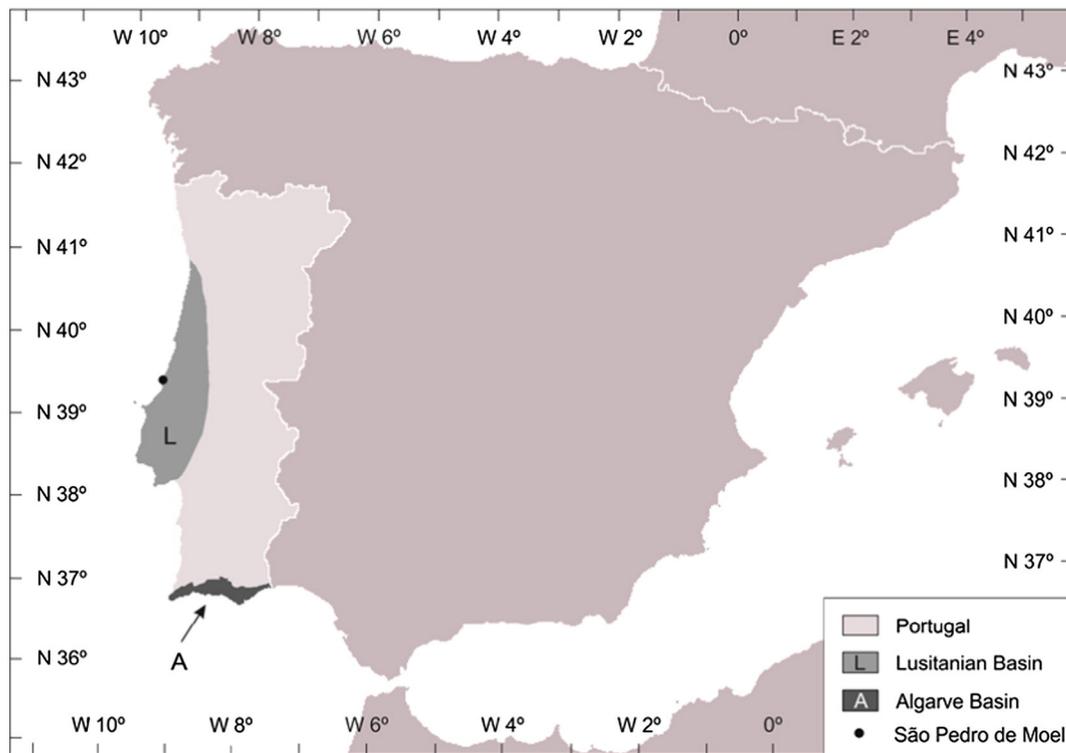


Fig. 1. Map with the location of the areas under study. The Lusitanian and Algarve Basins are highlighted.

Many of those species were described for the first time in Portugal. In the majority of cases, the observed fossils belong to old collections (late 19th to early 20th century), making it difficult to establish a precise age distribution in many cases. The fossil ages provided by old publications often require revision, providing ages at stage level and, therefore, poor age range precision. For the diversity analysis and when a more restricted range was required, it was considered that the taxa in question would occupy the entire stage/substage interval. In total, 243 species were collected in the Lusitanian basin, 13 species in the Algarve basin, and 5 species common to both basins. These numbers demonstrate a remarkable difference in diversity signal from both basins, with only about 5% of species in the Algarve Basin.

The differences in the numbers of species between the two basins are significant. The Algarve basin has been historically less sampled than the Lusitanian basin, with many of the geological surveys and subsequent works focusing on the former basin. This fact can explain the difference between the palaeodiversity numbers of the two basins, in association with possible longer hiatus periods experienced by the Algarve basin. For the sake of providing results that are as accurate as possible and minimizing possible collecting bias, we will consider only diversity data from the Lusitanian basin.

The Mesozoic sediments in the Lusitanian basin range in age from Induan (Early Triassic) to Maastrichtian (Late Cretaceous), while the echinoid occurrences span from Sinemurian (Early Jurassic) to Maastrichtian and provide the most complete echinoderm fossil record in Portugal. The specimen ages were revised, when possible, with the aid of the latest local stratigraphic information and long-term, independent dating of the relevant marine Portuguese formations (Dinis et al., 2008; Kullberg et al., 2013). The stage and substage time intervals used in the dataset follow the boundaries in Gradstein et al. (2012), except in some additional subsequent revisions to substage boundaries, which are cited separately below.

In the past, it was common practice to erect echinoid species based exclusively on isolated spine morphology. However, recent studies noted the potential for high morphological variability of this character in individual specimens, especially in cidaroids. Depending on its

position on the test, the spine can be long or short, but can also possess different overall shape and ornamentation. This means that a single echinoid species may possess different spine morphotypes, and this has resulted in the establishment of multiple synonymous species, many based on isolated spines. On the other hand, some echinoid groups show low spine plasticity, whereby the same spine morphotype may be present in different species. Therefore, species identified only on spine morphology are not reliable and are excluded in the current study, to avoid counting the same species twice. By focusing only on the Lusitanian basin, and excluding taxa identified solely from spine morphology, the final dataset used for the analyses consists of 195 echinoid species.

2.1.1. The “Lazarus effect”

Whereas taxonomic level does not much affect the palaeodiversity curves for sampled-in-range data, the effect is quite different for range-through plots. In these cases, missing data, especially “Lazarus taxa” (i.e., disappearance and reappearance of taxon in the fossil record), are incorporated, and the relative frequency and sizes of gaps can vary depending on completeness of documentation and taxonomic level (Fara, 2001). Such corrections can reduce some gaps in the fossil record, for example, gaps resulting from basin discontinuities, like those that will be noted in our data. To correct for this effect, the generic dataset was checked for possible gaps in each genus range. Whenever this occurred, those gaps were filled. Both the corrected and uncorrected datasets were assessed for correlation and time series models.

2.1.2. Collecting effort

A collecting effort curve, or discovery curve, has often been used as a means of assessing the rate of species description and the trustworthiness of the dataset. The objective is to investigate whether the number of species within defined parameters (taxonomic, geographic, temporal) is reaching saturation, or if many species still remain to be discovered from accessible outcrops. When the level of saturation is approached, the plot of species accumulation against research time overall generally is a sigmoid curve, i.e., initial low rates of discoveries, followed by a

rapid increase in the number of species added, and then a new slow rate. This new slow rate tends towards an asymptote, which represents a hypothetical maximum record of species for the defined sampling universe (Benton et al., 2011), and is limited by possible bias in the rock record.

The collecting effort curve for the Lusitanian basin echinoids was built through the compilation of the number of species against the year they were described based on numerous publications (Forbes, in Sharpe, 1850; Lorient, in Choffat, 1880; Lorient, 1884; Lorient, 1887–1888; Lorient, 1890–1891; Lorient, 1900; Lorient, 1905; Lambert, 1913; Lambert, 1915 to 1916; Rey, 1972; Vadet and Willie, 2002). The new species that resulted from B.C.P.'s taxonomic revision are also included in this curve. The collecting curve includes only those species that are currently regarded as valid, not the sum total of all species as described.

2.2. Sampling proxies

2.2.1. Formations

Previous authors have used a variety of parameters as sampling proxies to explain the diversity signal. Fossiliferous formation numbers has been widely used as a sampling proxy (Peters and Foote, 2001, 2002; Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011; Mannion et al., 2011; Upchurch et al., 2011; Benson and Mannion, 2012; Lloyd, 2012; Benson and Upchurch, 2013). This metric has been proposed as a good sampling proxy since it reflects multiple sampling controls, including rock area, thickness, lithological variation, and some aspects of human effort (Peters and Foote, 2001). Therefore, it should also provide a summary of amount of record (Raup, 1976), research effort (Sheehan, 1977) and lithological variability.

However, others argue that fossiliferous formation count is a poor sampling proxy (Crampton et al., 2003; Wignall and Benton, 1999; Peters, 2006; Smith, 2007a, 2007b; Peters and Heim, 2010; Benton et al., 2011; Dunhill, 2011, 2012; Benton et al., 2013; Dunhill et al., 2014b). These authors present five reasons for their critique as follows: 1) definitions of formations are arbitrary and they vary significantly with stratigraphic age, geography and environment; 2) formations tend not to correlate with rock volume, area of exposure or collecting effort; 3) they are largely dependent on facies heterogeneity; 4) they are partially redundant with palaeodiversity, both measures reflecting rock heterogeneity; and 5) their volume varies at least over eight orders of magnitude.

We compiled two formations datasets for the Mesozoic of the Lusitanian Basin (based on Dinis et al., 2008; Kullberg et al., 2013), one including all formations, and the other the purely marine formations (Appendix A). The inclusion of terrestrial and transitional facies may seem counterintuitive, as echinoids are exclusively marine animals, but many of the Portuguese Mesozoic formations contain both marine and continental facies, and we considered it best to include all possible settings for echinoids. In any case, we offer results based both on the full formations dataset, and the strictly marine formations dataset.

2.2.2. Facies heterogeneity

Habitat heterogeneity has been suggested as another factor influencing the diversity signal obtained from the fossil record. Each type of habitat results in the production and accumulation of different types of sediments, and the organisms living there are adapted to those conditions. Theoretically, a greater diversity of habitats may imply a higher number of species, leading to a higher diversity overall. Crampton et al. (2006) suggested that the number of formations might be a good estimator of this rock facies heterogeneity.

In this study, we use variation in sedimentary facies as an indicator of numbers of habitats. To calculate this indicator, the description of each formation was examined (described in Dinis et al., 2008; Kullberg et al., 2013) to establish which facies were more dominant.

The facies terms used were as follows: limestones and dolomites; marls; sandstones; mudstones; conglomerates and evaporites.

A subdataset with just marine facies was also created, excluding conglomerates, evaporites and parts of the sandy facies. This subdataset is similar to the facies division used by Smith and Benson (2013). All the truly marine formations yield macrofossils, implying that the marine facies curve also corresponds to a fossiliferous facies curve. The sum of the number of each facies through time is used as an indicator of facies variability and, thus, an indicator of habitat variability.

2.2.3. Outcrop area

Another proxy used in this study is the outcrop area, or map area, corresponding roughly to the area available for retrieving fossils. As noted before (Dunhill, 2011, 2012), there can be a substantial difference between areas of outcrop and exposure: exposure is strictly the area of rock available for study at the surface, whereas outcrop always represents a larger area on the map, including areas of non-exposure where the rocks are covered by soil, water, and human developments (roads, cities). In our case, we could not obtain data on exposure, but at least the outcrop areas are assessed within a limited geographic area in which the degree of concealment (i.e., the difference between outcrop and exposure) for each formation is roughly equivalent.

Previous studies have tested the relationship between diversity and outcrop area, with some favouring (Raup, 1972, 1976; Peters and Foote, 2001; Smith, 2001; Peters and Foote, 2002; Crampton et al., 2003; Smith and McGowan, 2007; Smith, 2007a; Smith et al., 2012; Smith and Benson, 2013) and others discarding this relationship (Benton et al., 2011; Dunhill, 2011, 2012; Dunhill et al., 2012, 2013, 2014a, 2014b). One explanation for the covariation of palaeodiversity and outcrop areas was that outcrop area is a metric of sampling, and rises and falls in both time series could simply record collecting opportunity rather than any real diversity signal (Smith, 2001, 2007a; Crampton et al., 2003). Alternatively, the covarying signals might reflect the common cause model (Peters, 2005; Hannisdal and Peters, 2011), a kind of species-area effect driven by sea level change, especially in the case of shallow marine formations, as here.

To test for covariation of palaeodiversity and outcrop area signals, the method of Smith and McGowan (2007) and Smith and Benson (2013) was used here. Their method consists in using the distribution grid of geological maps, together with the information from the map memoirs, to retrieve a count of how many grid units contain each fossiliferous formation. This method provides an even distribution grid through the area of study and provides even estimates of the formation area. These areas were then organized in sequence by time bins. Smith and McGowan (2005) tested this method at different map scales and concluded that the curve obtained had the same pattern, regardless of which map scale was used, just changing the amplitude of the peaks.

The Portuguese Geological Survey (Laboratório Nacional de Energia e Geologia, LNEG) produced geological maps at the scales 1:50,000, 1:200,000, 1:500,000 and 1:1,000,000. Unfortunately, both the Lusitanian and the Algarve basins are not fully mapped at the 1:50,000 and 1:200,000 scales. For this reason, geological maps at 1:500,000 and 1:1,000,000 were used, but subdividing these maps with the grid of maps of lower scale. This could be achieved by using an on-line tool called Geoportal (<http://geoportal.lneg.pt/geoportal/mapas/index.html>), provided by LNEG, where the geological maps can be interactively visualized at different scales and grids superimposed on other scales. At the usable scales mentioned above, the website provides coarse information, not providing information for each individual formation. Instead, it provides groups of units and their age ranges.

At the scale 1:1,000,000, the website provides groups of units, corresponding to coarse stratigraphic packages, and their age ranges at series level (Appendix A). On the other hand, maps at the scale 1:500,000 give a little more information. At this scale, the units comprise a mixture of formal and informal stratigraphic units, some of them correlated with established formations, again with a range at series level. To improve

the precision of the age range of each unit, the unit's descriptions were compared with the works of Dinis et al. (2008) and Kullberg et al. (2013) and, where possible, a more precise age range for each group of sedimentary packages was attributed. For this study, only data from sedimentary units were extracted, excluding the volcanic deposits from the end of the Cretaceous, which lack macrofossils. With the units established and their age ranges constrained, the distribution of each formation at both scales was extracted. For each map scale in use, the grid of the 1:50,000 geological maps was superimposed and the number of grid units in which each sedimentary group appeared was counted (Appendix A). At the scales used and the information provided by the used tool, it was not possible to determine the area for each individual formation, despite all efforts.

2.2.4. Palaeotemperature

Echinoids can provide important information about biotic and climatic evolution. Therefore, it is reasonable to compare the evolution of this group with climate parameters, like temperature. It has been suggested that temperature controls echinoid diversity, with cooling periods decreasing their global diversity (McKinney et al., 1992). Carbon and oxygen stable isotopes have been used as proxies for palaeoclimate signal (e.g., Voigt et al., 2003; Carpentier et al., 2006; Martin-Garin et al., 2010; Suan et al., 2010; Price et al., 2013), with both isotopic signatures providing information regarding warming or cooling periods. For this study, the isotope dataset was compiled from different publications (Saito and Van Donk, 1974; Price and Sellwood, 1994; Picard et al., 1998; Veizer et al., 1999; Voigt, 2000; Cresta et al., 2001; Wierzbowski, 2002; Voigt et al., 2003, 2004; Fursich et al., 2005; Carpentier et al., 2006; Aguirre-Urreta et al., 2008; Price and Teece, 2010; Suan et al., 2010; Huber et al., 2011; Lazar et al., 2011; Alberti et al., 2012; Armendáriz et al., 2013; Price et al., 2013), comprising a total of 1341 samples from different localities with a worldwide distribution, some of which are Portuguese localities. The isotopic signatures used were extracted from Mesozoic brachiopods, oysters and foraminifera, with no evidence for diagenetic alteration (Appendix A). The compilation of the dataset follows the criteria used by Price et al. (2013) and, therefore, information on wood, belemnite and bulk rock isotopes was discarded. The same authors preferred not to adjust the $\delta^{18}\text{O}$ values for secular variation, due to inconsistencies in the use of the 'carbonate clumped isotope' method, and preferred to use this proxy as an indicator of temperature changes, in which more negative isotope ratios indicate seawater warming. Bearing this in mind, a compilation of isotope ratios is here used as a proxy for temperature changes.

2.2.5. Sea level

Sea level change is another factor usually thought to influence diversity. This proxy has long been recognized as a potential driver of diversity changes, with sea level falls causally linked to extinctions (Chamberlin, 1909). Fluctuations in global sea level are a consequence of changes in the ocean water or oceanic basin volumes, linked with tectonic events and temperature changes. Later, Newell (1967) suggested a correlation between periods of loss of epicontinental seas during sea-level lowstands, and major palaeontological turnovers.

Further, with sea level rise, flooding of cratons occurs, increasing the area of shallow marine shelf available for organisms to occupy. This expansion of shallow waters promotes the area for marine sediment deposition, resulting in an increase in the rock record. On the other hand, regressions reduce the habitat area and the volume and surface area of previously deposited sediments, due to erosion. This coupling of shelf rock and fossil records can be interpreted either as evidence for a 'common cause' model in which both rock volume and fossil diversity rise and fall in concert because both are driven by sea level rises and falls (Peters, 2005). Alternatively, the very changes in sea level can be seen as controlling fossil preservation by erosion during transgressions (Smith, 2007b). McGowan and Smith (2008) found from cross-correlation analyses that there is some evidence for intercontinental

correlations, apparently linked to long-term sea-level fluctuations, at first and, occasionally, second-order cycles.

In the absence of a comprehensive local sea level curve, the Portuguese Mesozoic echinoid palaeodiversity was compared with two global sea level curves (Haq et al., 1987; Miller et al., 2005) and a western European sea level curve (de Graciansky et al., 1998). The raw data for the global curves was provided by Miller et al. (2005). The raw data for the de Graciansky et al. (1998) sea level curve could not be obtained.

Because the raw data for this last curve are not provided, the Grabit tool in the Matlab program (Doke, 2007) was used to extract point values from the figure provided by de Graciansky et al. (1998, Appendix Chart 1) and extracted as many points as needed to replicate the original curve. The output of the program is a file with the x and y coordinates of each point (see Appendix A).

2.3. Generating the diversity, formations, facies and outcrop curves

The diversity, formations, facies and outcrop values through time were calculated and plotted in R v.2.14.1 (R Development Team, 2013) using a script created by B.C.P. (see Appendix B), using part of Graeme Lloyd's 'rt_diversity_ranges.r' script. This script divides the time frame into equal time bins and searches through the dataset for taxa that occur within each time bin. For our analysis we used a time bin bandwidth of 1 Myr.

Currently, there are two commonly used methods to address the issue of plotting diversity through time, the use of time bins or the use of arbitrary bins, like stages or substages. The first method is highly dependent on the precision of the dataset, but tries to be a faithful representation of reality. The second method overestimates diversity by stating, for example, that a certain species that could have lived for 5 Ma, actually spanned just 2 Ma. Also, the use of stages, or substages, implies extra mathematical corrections, for addressing the uneven time distribution of those categories. With these differences in mind, the time bin projection was chosen, to try to obtain the highest precision possible.

2.4. Pairwise the datasets

The oxygen isotope, carbon isotope and sea level datasets did not possess the same time bin distribution as our diversity dataset. The statistical methods that we used can only be performed if all datasets are distributed in the same time bins (paired). For the isotopic datasets, the function 'ksmooth' in R was used to create a smooth line based on the full set of irregularly spaced isotopic values. For this curve, we used a bandwidth of 10 Myr.

Then, functions based on the isotopic and sea level curves were created, through the 'splinefun' function in R, using the method 'monoH.FC'. After the different functions had been created, the values for each diversity time bin midpoint were extracted, and these were used for time series and correlation comparisons with the diversity values for each time bin (Appendix B).

2.5. Generalized differencing

The palaeodiversity signal and tested sampling metrics were initially considered as raw values and then subjected to generalized differencing. This manipulation of the data aims to remove general background patterns ('detrending'), by identifying any trends in the data, through a linear model, and the differences from it. This data transformation was carried out in R, using Graeme Lloyd's script 'functions_2.r' (Lloyd, 2008) together with an automated R code, written by B.C.P. (Appendix B). This data manipulation was previously used by, for example, Benson and Butler (2011), Benton et al. (2013) and Smith and Benson (2013).

2.6. Pairwise correlation analyses

Spearman rank correlation tests were performed to explore covariation between the palaeodiversity data and the different sampling and environmental proxies. The strength of such correlations indicates the extent to which each variable might explain part of the diversity signal variance.

Then, to circumvent the possibility of redundancy between sampling proxies, correlation tests between the proxies were performed. If the correlation was high between two proxies, that would imply that the proxies were based on the same signal and, in consequence, one of them should be excluded. All correlation tests were also performed in the program R, using a script developed by B.C.P. (Appendix B). This script uses the R function 'cor.test' to perform the correlation analyses, with the Spearman correlation method, and also corrects the results for false discovery rate. For this correction, the more strict Bonferroni method was used.

2.7. Generalized least squares model fitting

Correlation tests can only compare two variables at a time, for example, palaeodiversity with one sampling proxy or environmental driver. However, a modelling technique can investigate the explanatory power of each variable independently and the possibility of combinations. Such modelling approaches were previously used to assess palaeontological data (e.g., Marx and Uhen, 2010; Benson and Butler, 2011; Benton et al., 2011; Butler et al., 2011; Benson and Mannion, 2012; Benton et al., 2013; Smith and Benson, 2013). This study uses the generalized least squares (gls) model, based on the assumption that the values of the response variable are dependent, and common to ecological data across space and time. This method is commonly used to model correlated observations, which was assumed in the case of our data and proxies.

For this method, the 'gls' function in the 'nlme' library (Pinheiro et al., 2004) in the R program was used, on the raw data measures. To use this function, an R script was written by B.C.P. (Appendix B). Initially the routine was run with all putative explanatory variables together. Subsequently, the variables were gradually removed, one at the time, and different combinations were tested. For the initial analyses, tests were carried to determine which was the best autoregressive order value (p) in corARMA for our study. These tests used the diversity data at species level, $p = 1, 2, 3, 4, 7, 8$ and 20, in a model that considered several proxies under study (total formations, marine formations, oxygen isotopes, carbon isotopes and a global sea level). They were performed separately for diversity based on species, genera and genera corrected for Lazarus effect curves, and used the sea level curve based on the Haq et al. (1987) data.

As expected, some of the variables explain the variance in the response variable better than others, as measured by Akaike Information Criterion (AIC) values. According to Burnham and Anderson (2002), the Akaike Information Criterion corrected (AICc) values should be used instead of the AIC, when the number of observations divided by the number of estimated parameters is lower than 40. For our study, this fraction is definitively higher than 40. Nevertheless, the AICc values were also extracted, using the function 'AICc.gls' in the R library 'AICcmodavg' (Mazerolle, 2012). Lower AIC or AICc values can be interpreted as indicating better models.

3. Results

3.1. The collecting curve

The collecting curve of the Lusitanian basin (Fig. 2) shows that the rate of discovery of echinoids appears to have reached a steady state. Accumulation of new taxa showed significant growth during the late 1890s and early 1900s, especially by the work of Perceval de Loriol

(1828 to 1908). After this author, few articles were published, but these have added only a few new species and genera. This pattern of the curve suggests that there can be some confidence in the dataset and conclusions extracted from it.

3.2. Palaeodiversity through time

The comparison of the diversity curves at species, genus and family level shows that the pattern of the echinoid diversity curve is the same, independent of taxonomic level (Fig. 3A). The curves differ in the amplitude of peaks and in a slight smoothing of the curve at higher taxonomic levels. Plots of species through time changed relatively little with taxonomic revision, whereas the generic plots changed significantly. Changes in the generic assignments of many of the species arise because the old taxonomic assignments in the late 19th century have not subsequently been revised.

In the Lusitanian basin, the number of taxa varied significantly during the Mesozoic (Fig. 3A). The palaeodiversity curve is far from having a general trend, instead being characterized by peaks of diversification and drops of apparent extinctions. Many of these drops in diversity coincide with well-established basin discontinuities (Fig. 3B), and seem to indicate some sort of cause and effect. The time with most species is the Late Jurassic, standing out quite clearly on the diversity curve, and is preceded by the Callovian to Oxfordian hiatus (Kullberg et al., 2013). Also, the existence of marine formations is not indicative of the presence of echinoids. For example, during a great part of the Pliensbachian and part of the Toarcian there are no records of echinoids, even though a considerable number of marine formations existed during those ages (Fig. 3C).

3.2.1. Regular vs irregular echinoids

Regular and irregular echinoids show rather different palaeodiversity histories through the Mesozoic (Fig. 4A). These changes in the diversity of both groups might be related to changes in sedimentation type in the basin. The Jurassic of the Lusitanian basin is dominated by carbonates and mudstones, associated with a calm and tropical environment, while the Cretaceous was much more siliciclastic, with accumulation of mudstones, sandstones and marls. This change in the type of sedimentation could have led to environmental adaptation of the echinoids, inducing the diversification of endobenthonic forms, which are especially characteristic of the irregular echinoids.

3.2.2. Corrected palaeodiversity curves

The imprecision of echinoid classifications based on isolated spines was previously mentioned. Inclusion or exclusion of species based on spines has significant impact on the sampled diversity values. Removal of spine-based species significantly decreases the diversity of several times, especially during the Late Jurassic and Early Cretaceous. The higher impact of this subtraction on Jurassic than on Cretaceous diversity can be explained by the fact that regular echinoids were more abundant than irregular echinoids during the Jurassic. Regular echinoids have larger and more conspicuous spines, such as the cidaroids, while irregular echinoids have smaller and undifferentiated spines. Nevertheless, the overall diversity pattern remains the same with or without these species (Fig. 4B). Correlation tests (Appendix A) confirm the similarity of the two curves, whether assessed on raw data ($\rho = 0.964$, $p < 0.001$) or on data after generalized differencing ($\rho = 0.832$, $p < 0.001$). Therefore, it is preferable to use the dataset without the doubtful taxa, bearing in mind that this curve represents a minimum estimate of diversity.

When range data are calculated by filling gaps, to avoid the Lazarus effect at the species level, there are few changes in the palaeodiversity curve, with the ranges of only three species changed. On the other hand, at the level of genera, there are significant changes (Fig. 4C), presumably because there were many changes to total ranges when Lazarus gaps were filled. In particular, many drops are removed or significantly attenuated, that had previously been demonstrated to be

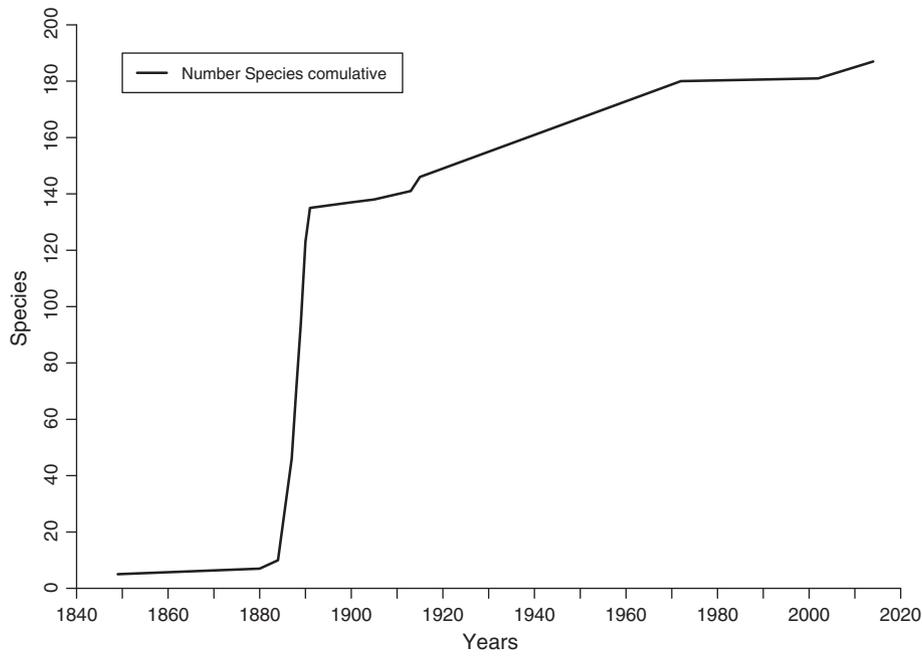


Fig. 2. Cumulative collectors curve of echinoid species descriptions through historical time, for the Lusitanian basin. Taxa based on spine morphology excluded.

associated with major basin discontinuities. Nevertheless, important and long temporal decreases in diversity are still well marked at the end of the Kimmeridgian and Hauterivian, even after correction.

Although the global disappearance of a taxon cannot be undone, the Lazarus effect can be circumvented. The local extinction of a certain taxon can precede recolonization from other habitats.

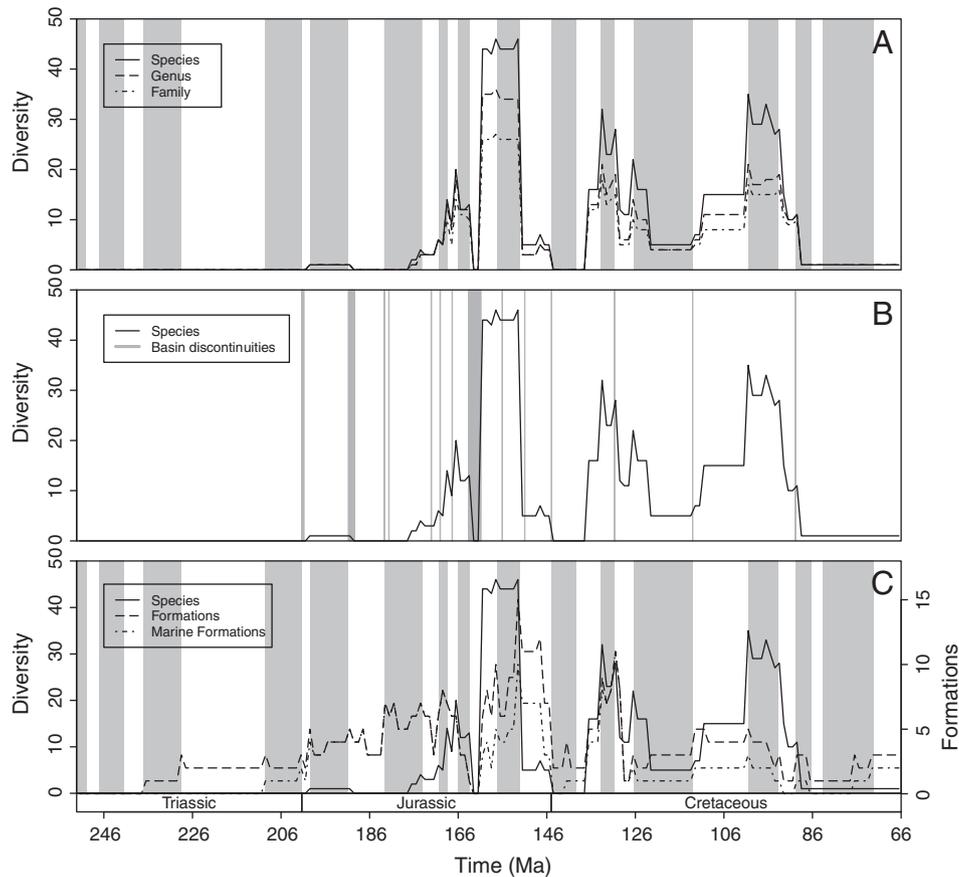


Fig. 3. (A) Echinoid species (solid line), genera (dashed line) and family (dashed dotted line) diversity, after removing species based on spine morphology, in the Mesozoic of the Lusitanian Basin. (B) Echinoid species diversity, after excluding species based on spine morphology (solid line) and major basin discontinuities (dark grey rectangular zones), after Kullberg et al. (2013), in the Mesozoic of the Lusitanian Basin. (C) Echinoid species diversity (solid line), excluding species based on spine morphology, total number of formations (dashed line) and number of marine formations (dashed and dotted line) for the Mesozoic of Lusitanian Basin. The grey rectangles represent the stages.

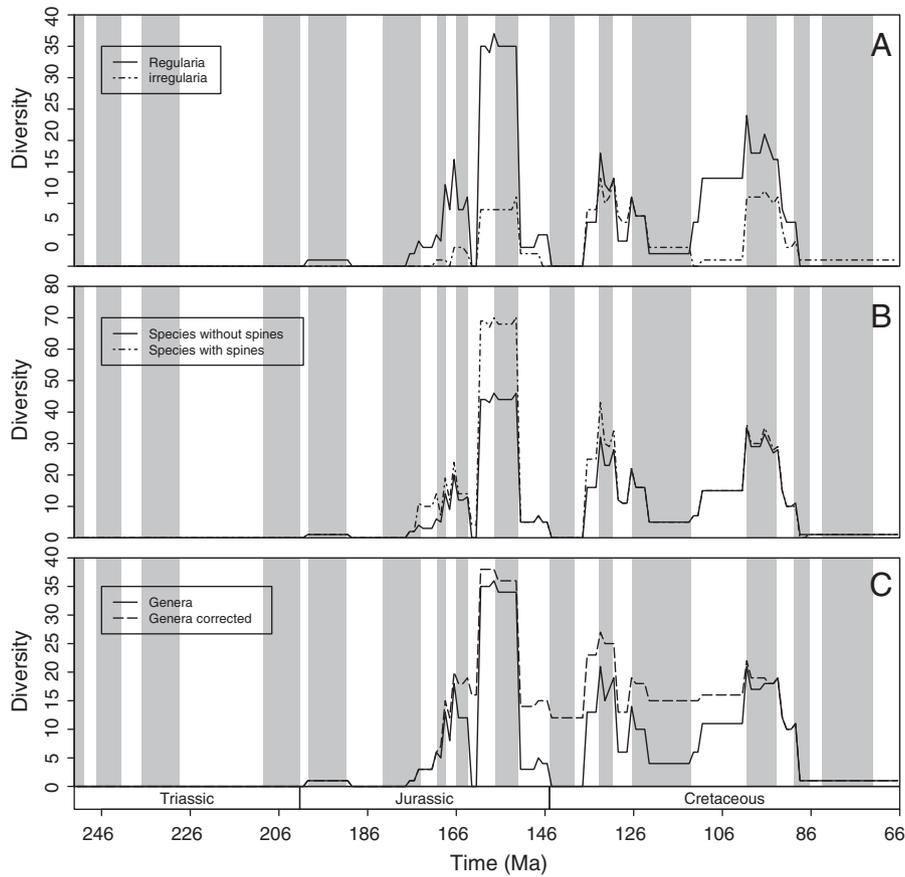


Fig. 4. (A) regular (solid line) and irregular (dashed line) echinoid species diversity, in the Lusitanian Basin, after excluding taxa identified based on spine morphology. (B) Number of echinoid species described for the studied time period (solid line) and number of echinoid species, when excluding the species described/identified on spine morphology (dashed line), for the Portuguese Mesozoic. (C) Echinoid diversity at genera (solid line) and corrected genera for the Lazarus effect (dashed line) curves, in the Mesozoic of the Lusitanian Basin. The grey rectangles represent the stages.

In our analyses, corrections for the Lazarus effect artificially attenuated many decreases in diversity. However, these corrections did not always produce improvements in correlation, slightly increasing it in some cases, but decreasing it in others (Appendix A). This raises the question of when it is appropriate to correct for Lazarus gaps. Generally, it makes sense to perform such corrections because the objective is to establish the best possible estimate of the overall palaeodiversity. The fact that the uncorrected palaeodiversity time series correlates better with the rock metrics than the corrected palaeodiversity signal confirms that some at least of the Lazarus gaps arise from inadequacies of sampling, as might be expected.

3.3. Sampling variables

3.3.1. Number of formations

In a few sections of our diversity plot, drops in diversity seem to be associated with decreases in the number of formations (Fig. 3C). For example, the Hauterivian diversity decrease is linked to a decrease in the number of both marine and total number of formations. The decrease of both diversity and number of formations is associated with the D13 basin discontinuity, which occurred in the Barremian, and corresponds to a regression maximum, which led to the general emersion of the Lusitanian Basin (Kullberg et al., 2013).

There is low to moderate correlation between palaeodiversity and total number of formations ($\rho \approx 0.4$ and $p < 0.001$, for both raw data and after generalized differencing), and with number of marine formations (Table 1; Fig. 3C; Appendix A). For both raw data and after generalized differencing, the correlation between diversity and

formations is slightly higher at lower taxonomic levels, even after applying the corrections against the Lazarus effect. After generalized differencing of the data, the correlation values between palaeodiversity and number of formations slightly increase, suggesting moderate values of correlation. On the other hand, the number of marine formations shows the same behaviour, but with considerably lower values (Table 1 and Appendix A). The application of generalized differencing slightly improves this correlation.

3.3.2. Facies heterogeneity

As for the diversity signal, the number of all facies and marine facies varies through time. The curve for number of facies per time bin does not have a specific trend, showing peaks and troughs (Fig. 5A). The same pattern is also observed in the marine facies curve.

The Spearman's rho values obtained for comparisons of time series of facies or marine facies and diversity indicate little to moderate correlation (Table 1 and Appendix A), at the levels of species, genera and corrected genera. The correlation values obtained for a simple correlation between diversity and facies were moderate ($\rho \approx 0.6$ and $p < 0.001$), while the same correlation, after generalized differencing, gave systematically lower rho values ($\rho \approx 0.35$ and $p < 0.001$). Further, the correlation between diversity and just marine facies retrieved systematically slightly lower values, for both raw data and after generalized differencing.

3.3.3. Outcrop area

The amount of sedimentary rock corresponding to the different time bins is not evenly distributed in the Lusitanian basin: the Cretaceous

Table 1
Correlation coefficients (Spearman's rho, ρ) and p-values between the palaeodiversity and the different proxies, at species level. The palaeodiversity signal refers to the diversity of the Lusitanian Basin, excluding taxa identification based on spine morphology. Values in bold represent statistically significant p-values.

Comparison	Spearman test		Generalized differences + Spearman test	
	ρ	p-Value	P	p-Value
Diversity \times total number of formations	0.3478908	<2.2e-16	0.4750611	<2.2e-16
Diversity \times number of marine formations	0.1424233	1.773e-07	0.2783111	<2.2e-16
Diversity \times all facies	0.6349632	<2.2e-16	0.337582	3.004e-06
Diversity \times marine facies	0.5643569	<2.2e-16	0.3516584	1.086e-06
Diversity \times outcrop (1:1,000,000)	0.4052215	9.622e-09	-0.05812138	0.4316
Diversity \times outcrop (1:500,000)	0.6965468	<2.2e-16	0.3668568	3.429e-07
Diversity \times δ^{18} oxygen	0.1746603	1.36e-10	-0.006837237	0.8031
Diversity \times δ^{13} carbon	0.2074738	1.991e-14	-0.04681501	0.08765
Diversity \times sea level (Haq et al., 1987)	0.2958423	<2.2e-16	-0.04797601	0.08006
Diversity \times sea level (Miller et al., 2005)	0.3293531	<2.2e-16	0.02278169	0.4061
Diversity \times sea level (de Graciansky et al., 1998)	0.3005157	<2.2e-16	-0.05214827	0.05707
Diversity \times outcrop (1:500,000) + marine facies	0.7253658	<2.2e-16	0.4631989	4.165e-11
Lusitanian \times U.K. species diversity	0.2952271	0.3515	0.4363636	0.1825

time bins show generally higher outcrop areas than the Jurassic time bins (Fig. 5B). Correlations between diversity and outcrop area change markedly according to the map scale. The outcrop dataset based on the maps at 1:500,000 systematically yielded better correlation values than those based on the 1:1,000,000 scale (Table 1 and Appendix A). The correlations between diversity and outcrop area based on geological maps at the scale 1:500,000 yielded high (raw data, $\rho \approx 0.7$ and $p < 0.001$) and moderate (generalized differenced, $\rho \approx 0.4$ and $p < 0.001$) rho values.

3.3.4. Diversity and sampling proxies

Different correlation test results were obtained from the comparison between diversity and the rock record proxies. The correlation between formations and marine formations, formations and marine formations with facies and marine facies retrieved high rho values, for the raw data and moderate values, after generalized differencing (Table 1 and Appendix A). This shows that these proxies share a common trend and should be tested separately, implying that substantial redundancy exists between some pairs of these proxies. Also, the correlation tests

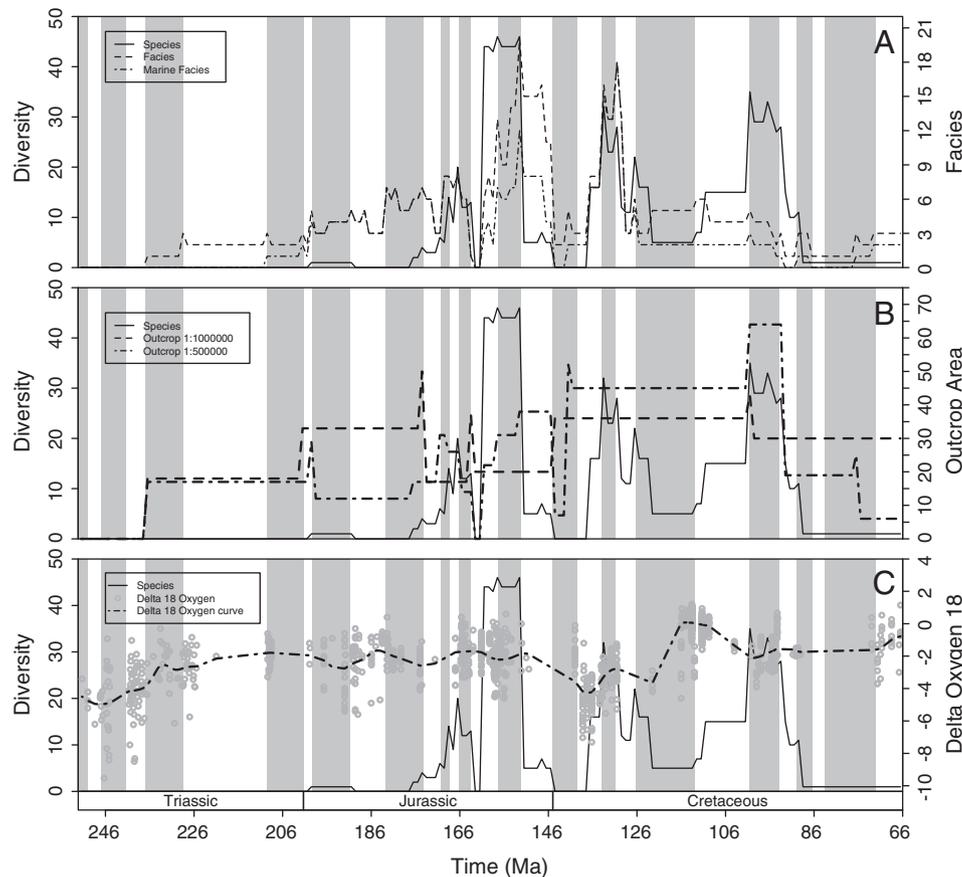


Fig. 5. (A) Echinoid species diversity, after removing species based on spine morphology (solid line), with the facies (dashed line) and marine facies (dashed dotted line) variation for the Lusitanian Basin. (B) Echinoid species diversity without species based on spine morphology (solid line), with the outcrop area based on the geological maps at the scale 1:1,000,000 (dashed line) and 1:500,000 (dashed dotted line). (C) Echinoid species diversity, after removing species based on spine morphology (solid line), in the Mesozoic of the Lusitanian Basin, isotopic values of δ^{18} oxygen of brachiopods, oysters and foraminifera (grey dots) and the smooth curve generated with the Kernel regression method, with a bandwidth of 5 Myr (dashed dotted line).

between facies and marine facies with outcrop area (1:50,000) were associated with moderate rho values (around 0.30), for both raw data and after generalized differencing. Although a moderate correlation, these values appear to suggest a common factor influencing both proxies, and the results extracted from them should be interpreted carefully.

The rock proxies that showed consistently the highest correlation values with diversity (at all taxonomic levels tested) were facies variation, both total number and just marine facies (Table 1 and Appendix A). This moderate correlation remained similar after applying generalized differencing to the data. This implies that, as with the previously mentioned studies, facies heterogeneity might have some control over the biological signal obtained from the geological record, or that the sampling across facies is influencing the diversity signal. Sedimentary facies are highly dependent on environmental factors, which also influence diversity. Higher numbers of habitats produce higher numbers of facies and, also, hold potential for higher rates of diversification. These higher rates of diversification are linked to the potential for new habitats to be occupied by different species. It was surprising that the total number of facies had a slightly higher correlation with diversity, than did marine facies alone. The reason for this could be that by using just marine facies variation, we are not encompassing the full range of habitats in a particular time period. For example, by focusing on just marine facies, transitional environments that, at some point, could have held echinoids are excluded. Therefore, by just focusing on marine facies we are excluding the full range of habitats.

On the other hand, the correlation values between palaeodiversity and the number of formations and marine formations is considerably less significant, for both raw data and after applying generalized differencing (Table 1 and Appendix A). The results of the Spearman

correlation tests are significantly lower than those obtained for the other rock proxies, with the correlation slightly increasing after generalized differencing, at all taxonomic levels tested (Table 1 and Appendix A). The expansion or contraction of marine habitats related with sea level changes would lead to variation in the number of marine formations, due to changes in sedimentation style. The correlation values obtained seem to support this idea.

The raw correlation between diversity and outcrop area yielded different correlation values, according to the map scale used. While for maps at 1:1,000,000, the correlation values were weak, for the scale 1:500,000, the correlation was significantly stronger (Table 1 and Appendix A). On the other hand, after applying generalized differencing, both scales were associated with quite low correlation values. These low correlation values appear to indicate that the diversity signal obtained by fossil counting is not biased by an accessibility factor, but on outcrop alone. If that bias existed, time periods with larger outcrop areas would have yielded more fossils and vice versa, and the correlation between diversity and this proxy would be high. Nevertheless, the influence of sampling area cannot be entirely excluded.

3.4. Environmental proxies

3.4.1. Temperature driver

From the observation of the two isotopic ratios, it seems that there were no significant long-term temperature changes (longer than 10 Myr, which is the bandwidth for projecting the data), during most of the Mesozoic, since both oxygen and carbon isotopic signatures do not show major fluctuations (Figs. 5C and 6A). Isotopic values indicate that global temperature was significantly warmer than today, since the

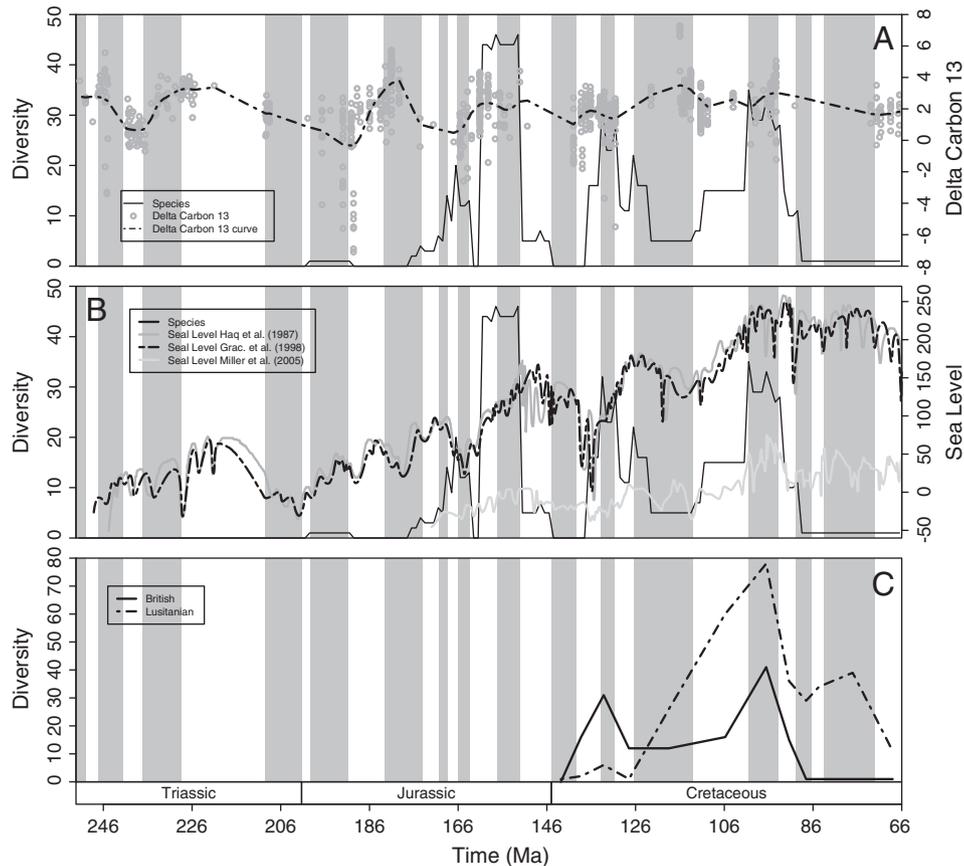


Fig. 6. (A) Echinoid species diversity, after removing species based on spine morphology (solid line), in the Mesozoic of the Lusitanian Basin, isotopic values of δ^{13} carbon of brachiopods, oysters and foraminifera (grey dots) and the smooth curve generated with the Kernel regression method, with a bandwidth of 5 Myr (dashed dotted line). (B) Echinoid species diversity in the Mesozoic of the Lusitanian Basin (solid black line) and global sea level curves based on Haq et al. (1987), de Graciansky et al. (1998) and Miller et al. (2005) (light grey line). (C) Comparison between the Portuguese (solid line) and the U.K. (dashed line) Cretaceous echinoid diversity.

oxygen isotopic ratios are more negative and the carbon isotopic ratios are higher than the present day. For example, Myers et al. (2012a, 2012b) show a surface palaeotemperature for the upper Kimmeridgian/lower Tithonian Lourinhã Formation between 27 °C and 34 °C (average 31 °C).

There is very little correlation between palaeodiversity and both isotopic curves (Figs. 5C and 6A; Table 1 and Appendix A), especially after applying generalized differencing ($\rho \approx 0.10$ and normally $p > 0.003$), suggesting that temperature had little influence on echinoid palaeodiversity. It is unclear whether this is an artefact of imprecise data, or an indication that the temperature of seawater does not affect echinoid diversity.

3.4.2. Sea level driver

The three sea level curves used in this study (Haq et al., 1987; de Graciansky et al., 1998; Miller et al., 2005) show overall trends of increase of sea level through the Mesozoic, but with different orders of magnitude (Fig. 5C), and agree on an apparent overall trend for a stabilization of sea level during the Late Cretaceous. This overall trend of increase in sea level is punctuated by small drops, which vary in magnitude according to the model chosen and do not always coincide between models.

Correlation tests between palaeodiversity and the sea level curves (Table 1 and Appendix A) produced rather low Spearman's rho values, both for the raw ($\rho \approx 0.2$ and $p < 0.001$) and generalized differenced data ($\rho < 0.1$ and $p < 0.001$). The results vary slightly according to the taxonomic level chosen. For the raw data, the highest correlation values were obtained between species and Miller's curve. Regardless of the taxonomic level chosen, Miller's curve yielded the highest values, while Graciansky's resulted consistently in the lowest values. Looking at the generalized differenced correlations, the results were not always statistically significant, yielding significantly lower rho values than the raw data comparisons. Also, the results vary according to the taxonomic level chosen, decreasing with higher taxonomic levels.

3.4.3. Diversity and the environmental proxies

The low correlation values between diversity and sea level could result from the fact that none of the curves used truly corresponds to the sea level variations, in the Lusitanian Basin. In this basin, sea level was controlled by global/regional sea level changes, but also by local tectonic events, that would have played an important role in determining the area of continental flooding. Also, this low correlation appears to go against the "common-cause" hypothesis. For this hypothesis to be true, we ought to obtain a correlation between sea level and diversity, which is not the case in this study.

As previously noted, temperature changes had little influence on palaeodiversity, going against the common view that echinoids are a good proxy for inferring palaeotemperature (e.g., McKinney et al., 1992). This result is also opposite to the findings of Mayhew et al. (2008, 2012). These authors demonstrated that temperature correlated with different measures of palaeodiversity at global scale, although in different ways (with highs in palaeodiversity either correlated with lows or highs in palaeotemperature). But, it must be borne in mind that that study was made across the entire Phanerozoic and, by consequence, used broader and less precise data. Again, the regional-scale records ought to show this correlation even more convincingly, if the relation between temperature and diversity exists. Perhaps the analyses by Mayhew et al. (2008, 2012) provide evidence for correlations because of summing effects of randomly varying regional-scale data sets, and there is in fact no evidence that palaeotemperature drives global palaeodiversity. To sum up, it appears that both environmental proxies analysed had very little influence on the palaeodiversity.

3.5. Model fitting analysis

Before the model analyses were performed, the possibility of convergence between proxies was investigated. The use of two variables with the same behaviour would bias the results of the model towards that signal. To circumvent this, correlation tests were undertaken between the different variables. Please, see Appendix A for the results of such tests. When the correlation results between two variables were high, these variables were used in separate models.

From tests performed to investigate the best autoregressive order value (p), the value of p that retrieved the lowest AIC value was 1 (Appendix A). The remaining orders not only resulted in lower AIC values, but also substantially increased the time required for computation. In consequence, all subsequent tests used 1 as the value of p . For tests using $p = 2$ and 3, the program reported an error.

For the diversity data at species level and using all meaningful proxies (marine formations, marine facies, outcrop at 1:1,000,000 map scale, oxygen and carbon isotopes, de Graciansky et al., 1998 sea level curve), it is clear that the only proxies with a meaningful p -value (values of 0) are facies heterogeneity and outcrop area. All other proxies show rather higher p -values (above 0.05), suggesting a lower correlation of these proxies with palaeodiversity. After this initial test, other possible models were assessed in different combinations, by removing and adding proxies. Constant to all models were that the marine facies counts and outcrop areas (at the scale 1:500,000) showed highly significant correlations with palaeodiversity ($p < 0.001$). The coefficient values between palaeodiversity and these two proxies are positive (Appendix A), in combination and isolated. This indicates that, when outcrop area and marine facies heterogeneity increase, the number of species retrieved also increases.

The model fitting analyses show a similar result to the correlation tests. In all the models calculated, the isotopic and sea level variations appear to have had very little influence on the diversity signal, with the coefficient values varying according to the proxy. Nevertheless, it is possible to infer that the increase of temperature might have allowed an increase in diversity. The carbon isotopic signature systematically yielded positive coefficients while the oxygen isotopes were constantly negative. Although the two proxies have opposite signals with respect to diversity, they both point to the same behaviour. With temperature rise, the carbon isotopes tend to be more positive and the oxygen more negative. So, and even if the models indicate that temperature had very little influence on diversity, the rises in temperature seem to be associated with a small rise in diversity.

While the relation between temperature and diversity seems to have some trend, the model fitting analyses for the sea level curves have no particular direction. The coefficient values for sea level were low and with mixed signals, positive in some cases and negative in others (Appendix A). Also, the coefficient values were relatively low, which presumably relates to the uncertainty of the signal.

Different models were also run with the objective of understanding which proxy explained more of the palaeodiversity time series, whether marine facies heterogeneity or outcrop area (at the scale 1:500,000). In sequence, the model fits for single proxies with the lowest AIC values (Appendix A) are marine facies, then all facies, and then outcrop area. All the other models with the proxies under study resulted in higher AIC values and higher p -values (Appendix A). The same models were calculated with diversity based on genera and genera corrected for gaps in the record. At corrected generic level, the AIC values were smaller than for the same models with diversity at species level (3855.082, tested with marine facies and outcrop area 1:1,000,000). Other combinations of models at different taxic levels and without corrected palaeodiversity data provided higher AIC values, and so are not included here. The AIC values were also obtained for several of the models but the differences between the AIC and AICc values are minimal and, therefore, neglected here.

The model fitting analyses (gls) allowed better understanding of the relationship between the rock proxies and palaeodiversity. Facies and

marine facies are the proxies that yielded the best scores, with highly significant p-values of 0 (Appendix A). The different models showed different directionalities between diversity and proxies, according to the proxy in question. The coefficients were systematically positive for facies, marine facies and outcrop at the scale 1:50,000. On the other hand, outcrop at the scale 1:1,000,000 retrieved negative values, while formations and marine formations produced positive and negative coefficient values (Appendix A).

The model that yielded the lowest AIC value included marine facies and outcrop area, at the scale 1:50,000 (AIC = 5511.596), with both yielding p-values of 0. The coefficient value obtained from this model was higher for the marine facies count than for the outcrop area. The results for the other models are provided in Appendix A.

After the model fitting analyses, the two proxies used in the model with the best results were combined and correlated with palaeodiversity. The combination of marine facies and outcrop area resulted in moderate correlation values with the diversity signal, for the pairwise correlation tests (for the raw data and after generalized differencing) and model fitting. The two proxies combined resulted in better correlation values than for the two proxies isolated, and implies that both proxies in conjunction conditioned the diversity signal. Smith and Benson (2013) obtained a similar result for the Cretaceous echinoids of the U.K. However, the correlation values obtained by those authors were significantly higher. Possible reasons for this will be addressed below. A summary of the most relevant values obtained by the model fitting analyses can be found on Table 2.

The correlation between diversity and the combination of marine facies and outcrop area is significant. Nevertheless, interpretations of these correlations need to be cautious. The correlation tests between marine facies and outcrop area demonstrate the existence of some relationship between the two proxies, with rho values of 0.286 (raw data) and 0.353 (after generalized differencing), and suggest a common factor influencing both proxies.

3.6. Diversity, marine facies and outcrop area

The Spearman rank correlation tests (Table 1 and Appendix A) show variable rho values and a tendency to low p-values. Since the gls results indicate that marine facies and outcrop area (at the scale 1:500,000) were the proxies that best explained the diversity signal, these two proxies were further tested with the Spearman correlation test. This allowed comparison with the results of Smith and Benson (2013). In both cases, in Portugal and in the UK, these two proxies yielded the lowest AIC values of all tested models, suggesting that facies heterogeneity and outcrop area together best explain the palaeodiversity signal (Table 2).

With this result, we decided to further test the correlation between diversity and these two variables combined, by multiplying the marine facies signal with the outcrop curve. The same procedure was used by Smith and Benson (2013), and provides a proportion of the outcrop area of marine facies per time bin. The result was a stronger correlation (raw data) between diversity and the two proxies combined, but with variable rho values. The rho values for the raw data were systematically equal to, or lower than, those obtained for marine facies and outcrop area isolated, implying that the combined proxies provide the highest explanatory power (Table 1 and Appendix A). On the other hand, the correlation values after generalized differencing yielded significantly better results than those from the two proxies isolated, with consistently low rho values. This suggests that overall trends were obscuring some aspects of the finer-scale, bin-by-bin correlations.

4. Discussion

4.1. Palaeodiversity interpretations

In the Lusitanian basin, there are no records of echinoids in the Triassic, because sedimentation was predominantly terrestrial. The

Table 2

Comparison of generalized-differenced time series models between palaeodiversity and the proxies. The palaeodiversity signal refers to the diversity of the Lusitanian Basin, excluding taxa based only on spines.

Proxies	AIC	Coefficients	p-Values
All facies	5546.096	1.001621	0
Marine facies	5526.639	1.266207	0
Outcrop (1:50,000)	5628.395	0.178438	0
Outcrop (1:50,000) + marine facies	5511.596	0.104395	0
		1.15307	0

first marine incursion happened in the early Hettangian, while true and stable marine conditions only became established during the Sinemurian, with the development of a carbonate ramp (Kullberg et al., 2013). The first echinoids appeared in the Lusitanian basin only during the lower Sinemurian (Fig. 3B), cidaroid spine fragments from São Pedro de Moel, Marinha Grande (Coimbra Formation). These are synchronous with the first true marine incursions into the Lusitanian basin. Later, rocks from the middle Sinemurian yield the first identifiable echinoid remains.

During the Pliensbachian and most of the Toarcian, no echinoids were found in the Lusitanian basin. At the beginning of the Pliensbachian, there was a rapid deepening of the basin, with an inundation maximum in the *Margaritatus* zone (upper Pliensbachian), according to Kullberg et al. (2013). By the late Toarcian and onwards, the number of echinoid taxa slowly increased, with a few drops, until the end of the Callovian.

The Callovian to Oxfordian transition is marked by a stratigraphic hiatus at the basin scale, which lasted until the middle Oxfordian, producing a hiatus in the fossil record. This episode corresponds to an early event of tectonic inversion, restricted to the Lusitanian Basin (Kullberg et al., 2013). Echinoid diversity peaked during the Late Jurassic, to about twice the level seen elsewhere in the remaining time series.

A significant drop marks the Jurassic to Cretaceous transition in echinoid diversity. This absence can be partially explained by the absence of marine sediments during the early Berriasian (Fig. 3C).

After this echinoid diversity drop, diversity recovered to levels not as high as the Jurassic record. This new diversification event coincides with a great increase in the number of irregular echinoids (Fig. 4A). During the Aptian, there was a significant decrease in echinoid diversity, which lasted some time and is contemporaneous with the regional so-called "Aptian crisis" (Kullberg et al., 2013). After a progressive sea level rise initiated in the early Aptian, the Lusitanian basin received a rapid and high-energy influx of clastic material, transported by fluvial systems and eroding the lower layers, according to Rey (1972). This freshwater input would have had a major impact on the marine ecosystem, especially on stenohaline animals such as echinoderms. This environmental change may explain the significant decrease in echinoid diversity during great part of that stage.

During the Cenomanian, an extensive carbonate platform was established (Dinis et al., 2008), with, once again, conditions for the proliferation and diversification of echinoderms, including echinoids (Fig. 3A). By the end of the middle of the Late Cretaceous, the Lusitanian basin could no longer accommodate sediments and the sea retreated. The Coniacian to Campanian is marked by a shift in the sedimentation depocentre to offshore. Only small areas of the northern part of basin could support restricted shallow marine waters (Dinis et al., 2008), not ideal environmental conditions for echinoids, while the southern region suffered erosion. This restriction in the habitat could explain the poor diversity of echinoids for most of the Late Cretaceous.

After this narrative, it is clear that the evolution of the Lusitanian basin had a direct impact on the diversity signal obtained from the fossil record. As Smith (2007b) indicated, tectonic drivers change the basin's area and volume, which influences the areal extent of continental flooding and, therefore, directly the diversity of marine faunas, according to a kind of species-area effect. Also, these tectonic events imply changes in basin sedimentation. As an example of this, Fig. 3B

demonstrates a good correlation between many of the diversity drops with major basin discontinuities.

4.2. Comparing the Portuguese with the U.K. diversity

Smith and Benson (2013) found that the British Cretaceous echinoids also occupied a passive margin linked to the opening of the North Atlantic. The number of species in their study is slightly larger than the dataset here, and it is focused on the Cretaceous. Their dataset is divided into stages, which divides the data into uneven time bins and provides a coarser timescale than here.

In the U.K., echinoid diversity during most of the Early Cretaceous was relatively low, with fewer than 10 species per stage. During the Aptian, echinoid diversity greatly increased, a trend that continued until the Cenomanian. After this period of increase, diversity decreased to about half the level that it reached during the Cenomanian. The numbers of species remained more or less stable until the Maastrichtian, when diversity decreased significantly.

The comparison between Portuguese and U.K. echinoid diversity shows a few similarities and a few differences (Fig. 6C). While the Early Cretaceous record of the U.K. is rather poor in echinoids, with fewer than 10 species through most of this time period, the Portuguese record is rather diverse, with about four times more species. This changed during the Aptian, and from this stage onwards, U.K. echinoid diversity was significantly larger than the Portuguese. Similarly in both areas, the Late Cretaceous started with high diversity, decreasing afterwards. In order to be able to correlate the two echinoid datasets, we transformed our dataset to the stage level and performed the correlation tests applied for comparing our diversity signal with the proxies.

Echinoid diversity from the U.K. Cretaceous revealed a strong correlation between the diversity signal and the grouping of outcrop area and marine facies, for both raw data and for first differenced data. As previously mentioned, the same proxies used in combination and correlated with diversity yielded lower values, for both the raw and generalized differenced data. The difference between the correlation values obtained for the two studies could result from differences in the resolution of the datasets used. As mentioned before, Smith and Benson (2013) organized their data by stages and used the stage midpoint to plot the data, while our data is organized by substages and 1 Myr time bins. Also, our outcrop dataset is based on maps with a larger scale than Smith and Benson's (2013) study.

In order to understand how similar the Portuguese and U.K. faunas were, we decided to correlate the two diversity signals. If the two diversity signals were a reflection of the geological evolution of the different basins, in a sense, biased by the rock record, the correlation between the two diversity datasets should be low. On the other hand, if biological factors were strongly imprinted on the diversity signals, the correlations between the data from the two basins should be high. We converted our initial dataset to the frame of Smith and Benson's (2013) dataset and performed the same correlation tests between the two datasets as were done for the Portuguese data alone. The tests were done on both the raw data and after applying generalized differencing. The rho values obtained were low for the raw data, and moderate after generalized differencing, but with high p-values (Table 1 and Appendix A). The high p-values provide very little confidence to state that the two datasets are statistically different.

4.3. Common-cause vs megabias hypothesis

Two hypotheses seek to explain the apparent correlation between diversity and some sampling proxies, the common-cause and the megabias. Smith and Benson (2013) interpreted the strong correlation between the combined proxies and palaeodiversity as an indicator that the rock record strongly influences the diversity signal. They consider that the rock record is highly conditioned by periods of deposition and erosion, with erosion events obliterating information, thus the

diversity signal is a direct reflection of geology. We obtained similar results to Smith and Benson (2013), although with a less strong correlation between diversity and the combined proxies. Therefore, we could assume that the rock record, and its availability, controls the diversity signal and, therefore, supports the megabias hypothesis.

But, these results can also be interpreted as in favour of the common-cause hypothesis. The higher correlation obtained with diversity and the two proxies combined, in contrast to values for each proxy alone, could be a consequence of the moderate correlation values retrieved between marine facies and outcrop area. This moderate relationship could indicate a common factor influencing both proxies, which would be influencing diversity as well. The results of a strong correlation between diversity and facies area availability can also suggest a diversity control through the area of continental flooding, or area of habitat. For this to be true, a stronger correlation between diversity and sea level would be expected, something that this study did not reveal. Also, the generally poor correlation results (after generalized differencing) could argue against the idea that the correlation of fossil diversity and formation count provides evidence for megabiases, and that other factors may have had a more important role in controlling echinoid diversity. If true, local diversity signals should be intrinsically related with the number of formations at smaller scales. If this is not the case, as we suggest, then it seems that there may be some kind of summing effect, where numerous uncorrelated signals, when lumped together, produce an apparently reasonable correlation (Benton, 2012).

Other factors that might have influenced the diversity of this group have yet to be tested, such as predator–prey pressure, nutrient availability, or tectonics. Tectonics induces changes in the basin volume, in the area of continental flooding and, in consequence, influences the number of formations (Smith, 2007b). In sum, tectonics controls the overall amount and heterogeneity of the geological record that is preserved, as well as the quantity of fossil material that reaches us. As noted before, there is evidence for a relationship between the decrease in palaeodiversity and basin discontinuities (Fig. 3B), with diversity apparently decreasing close to these discontinuities. This fact to be true and not an artefact of the method used seems to support the common-cause hypothesis. Discontinuities in the rock record at basin scale result from tectonic uplift and/or sea level changes. Such events would ultimately cause the erosion of the rock record and shrinking and loss of habitats would precede it. This change in habitat distribution would influence the overall diversity prior to the discontinuity. Although clearly an important driver, tectonics is hard to quantify for use in correlation tests.

The very low correlation values are in line with the conclusions of other studies at regional and local scales (for example, Dunhill et al., 2012, 2013, 2014a, 2014b) and indicate that none of the factors assessed is, on its own, truly driving Portuguese echinoid palaeodiversity. Many previous studies have identified strong correlations between global diversity and the number of fossil-bearing formations (for example, Benson and Butler, 2011; Smith and Benson, 2013). On the other hand, our local study obtained similar results to other regional and local studies, where this correlation is poor. It would be good to identify definite cause–effect linkages, and these ought to be clear at local and regional scales, where exact matching between rises and falls in the time series under comparison ought to be evident.

5. Conclusions

Echinoid diversity during the Mesozoic in the Lusitanian basin is far from having a general trend, differing from previous global studies in other taxonomic groups. Many of the variations in diversity seem to be linked to basinal discontinuities and, therefore, with the evolution of the basin.

Comparison between the plots based on species, genera, and families suggests that diversity patterns are independent of taxonomic level.

The different levels show similar diversity patterns, differing only in the magnitude of the changes.

The two different testing methods used to investigate the influence of the different sampling proxies on the diversity patterns obtained similar results. Both Spearman and gls tests indicated poor to moderate correlation between many of the analysed proxies and the diversity patterns. Among the different proxies tested, marine facies variation together with outcrop area showed the highest correlation with the palaeodiversity data. Furthermore, both correlation tests and linear model fitting agree that the temperature and sea level changes appear to have had very little influence on echinoid diversity.

Acknowledgements

We thank G. Price for providing some of the isotopic data used in this study, Graeme Lloyd for providing some of the R scripts, and Andrew Smith, for his comments on this manuscript. BCP thanks Pablo Palacios, for his many discussions regarding many of the setbacks experienced with the R script, and all people's comments on this work provided during the last EEC meeting. This work was funded by the FCT doctoral training grant SFRH/BD/68891/2010 to BCP. We also thank our Editor, Professor Finn Surlyk, and two referees (Dr manabu Sakamoto and an anonymous reviewer) for their helpful comments. We also thank our Editor, Professor Finn Surlyk, and two referees (Dr Manabu Sakamoto and an anonymous reviewer) for their helpful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2015.02.014>.

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